

## Intergroup conflict in captive siamangs (*Symphalangus syndactylus*)

Thomas Geissmann

Anthropological Institute, University Zürich-Irchel,  
Winterthurerstr. 190, CH-8057 Zürich, Switzerland  
E-mail: thomas.geissmann@aim.uzh.ch

In this study, I describe the increase in territorial behaviour of siamangs kept in two adjacent cages after the formation of a new pair. The formation of a new pair resulted in a significant increase of a form of inter-group agonistic behaviour (“arm-pulling”), which occurred exclusively among animals of the same sex. The increase in conflicts cannot be fully explained by the simple increase in the number of these territorial animals, but appears to be directly influenced by the formation of a new pair.

### Introduction

In wild gibbons (*Hylobatidae*), conflicts may occur when two neighbouring groups come close together near the boundary separating their territories. During this time, males typically sit or hang and stare at each other from exposed positions in trees. Occasionally, they swiftly chase each other with vigorous movement. Females usually remain in the background but may vocalize and groom their male mates (Gittins and Raemaekers, 1980; Leighton, 1987). Disputes last from a few minutes to over two hours and about 40 minutes (Gittins, 1984) and may be accompanied by more or less intense calling by the male or by all group members. Territorial disputes are relatively rare in most gibbon populations, with rates varying between populations and over time from once every two days to as low as once a month (Leighton, 1987). Inter-group conflicts in wild siamangs (*Symphalangus syndactylus*) have been described by Chivers (1974). They are basically similar to disputes in other gibbon species but appear to be more rare (Brockelman and Srikosamatara, 1984).

Zoos only occasionally keep several gibbon groups of the same species in direct sight of each other, because this may increase rates of abnormal behaviour and heighten intra-group aggression (Ibscher, 1964). As a result, it is rarely possible to study territorial disputes in captive gibbons, where the only form of non-vocal territorial behaviour is usually directed at substitute territorial rivals such as humans (Orgeldinger, 1997).

Here I describe a particular form of territorial behaviour (i.e., arm-pulling) of siamangs kept in two adjacent cages. I recorded changes in the frequency of this behaviour before and after the formation of a new pair. Because the frequency of territorial disputes in wild gibbons reportedly is “much affected by the number of neighbouring groups, and especially by the appearance of new neighbours” (Gittins and Raemaekers, 1980, p. 75), I expected an increase in inter-group disputes after an adult male was added to the unmated female in one of the cages.

### Animals and methods

Observations for this study were carried out as part of a larger project on duet singing and pair bond strength in captive siamang groups (Geissmann, 1986, 1999, 2000).



**Fig. 1.** The adult siamang pair *Ra* (left) and *Bb* (right) at the Zoo Seeteufel in Studen, Switzerland. Photo: Thomas Geissmann. – *Das erwachsene Siamang-Paar Ra (links) und Bb (rechts) im Zoo Seeteufel in Studen, Schweiz.*

The study animals were kept in the Zoo Seeteufel in Studen, Switzerland (three groups). The original housing configuration consisted of one solitary adult female *Vr* (*Vreneli*), one adult pair *Bb+Ra* (*Bobby* and *Ratana*), and one family group. The male *Bb* of the adult pair *Bb+Ra* was wild-born

in about 1958 and thought to be infertile. The female of this pair was wild-born in about 1963. This pair has been together since July 1980 (Fig. 1). The solitary female *Vr* was wild-born in about 1963 and remained alone after her offspring and her mate both died in 1979. On 14 July 1981, the adult male *Na* (Narong) was transferred from another zoo to Studen. This resulted in the formation of a new pair *Na+Vr*. The arriving male *Na* was wild-born in about 1967 and had produced several offspring with previous mates.

All groups could hear each other during the entire year. During the summer, all three groups were kept in wire-mesh outdoor cages (25 m<sup>2</sup> x 2.5 m) equipped with several horizontal metal bars, ropes, and a wooden sleeping box. Cages one and two stood close together at a sharp angle. The closest distance between the cages (at the corners) was little more than one meter. Here I focus on conflict behaviour observed between the two groups kept in the neighbouring cages one and two.

Agonistic displays directed at the neighbouring group are termed **conflicts** in the following text. During conflicts, rivals often reached out with one arm through the wire mesh towards each other. If they both reached out as far as possible (i.e., up to their shoulders) they were able to grab each other by their hands, whereupon they would begin to pull with considerable force (Fig. 2). I call this behaviour **arm-pulling**.

An additional family group of siamangs was present in Studen but is ignored in the present study. The cage of the family group was located at a distance of more than 10 m from the other two cages. No conflict behaviour was observed in the third group, perhaps because the sight from the third cage to the other two cages was reduced by shrubs and trees.

During the winter, the siamangs were housed in a building. During that season, groups one and two were kept farther apart and no observations on conflict behaviour were possible.

Each conflict bout in groups one and two that included arm-pulling (described below) was counted as one event, independent of its duration or the number of repetitions of arm-pulling. Observations were carried out daily from dawn to dusk, during three blocks of several days each: (1) during the week before the arrival of the new male (7–14 July 1981), (2) during the week after arrival of the new male (15–21 July 1981), and (3) about 2 months after the male's arrival (3–4 Sept. 1981).

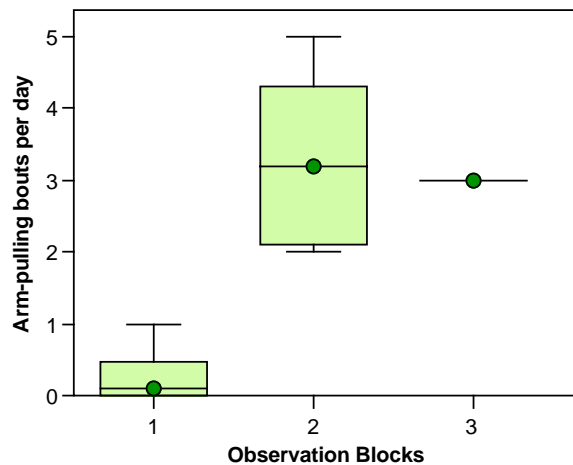
All statistical tests (Mann-Whitney *U*; Siegel, 1956) are two-tailed, with a significance level of 0.05.



**Fig. 2.** Arm-pulling between the adult male siamangs *Na* (left) and *Bb* (right) during a conflict between the pairs *Na+Vr* and *Bb+Ra*. Note how the wire mesh is deformed by the considerable force applied by the pulling animals. Photos: Thomas Geissmann. – *Armziehen zwischen den erwachsenen Siamang-Männchen Na (links) und Bb (rechts) während eines Konfliktes zwischen den benachbarten Paaren Na+Vr und Bb+Ra. Man beachte, wie der Maschendraht durch den Kraftaufwand der ziehenden Tiere nach aussen gedrückt wird.*

## Results

Before the arrival of *Na*, conflict behaviour (described below) had been observed only rarely and never reached the intensity level that was later observed. Arm pulling (also described below) was observed only once during the eight days immediately prior to the arrival of *Na* (0.1 events/day), and it occurred between the females *Ra* and *Vr*. In contrast, arm-pulling bouts occurred on average 3.3 times (range 2–5) during the eight days immediately after the arrival of *Na*. This difference is statistically significant (Mann-Whitney *U* test,  $p < 0.01$ ). A few small wounds were observed on the palms of *Na*; possibly, the males hurt each other with their fingernails during their arm-pulling behaviour. This did not appear to impede the frequency of arm-pulling. Even two months after the arrival of *Na*, neither conflicts nor arm-pulling (2 events/day) appeared to drop in frequency (Fig. 3).



**Fig. 3.** Arm-pulling bouts per day occurring between two siamang groups. The box plot shows mean, standard deviation, and range of the variable during three observation blocks: (1) during eight days immediately before the arrival of a new male at the zoo; (2) during eight days immediately after pair formation; and (3) during two days about two months after pair formation. – *Häufigkeit des Armziehens pro Tag zwischen zwei Siamanggruppen. Aufgetragen sind Mittelwerte, Standardabweichungen, und Maximum-Minimum-Werte dieser Variablen während drei Beobachtungsblocks: (1) während acht Tagen unmittelbar vor Ankunft des neuen Männchens im Zoo; (2) während acht Tagen unmittelbar nach Bildung des neuen Paares; und (3) während zwei Tagen etwa zwei Monate nach der Paarbildung.*

Several times during each day, the neighbouring pairs *Na+Vr* and *Bb+Ra* (cages one and two) engaged in mutual agonistic displays. These conflicts consisted of at least one member of each pair going to the corner of the cage where the distance to the opposite cage was shortest. Because there was only one corner in each cage where the opponents were able to touch each other, conflicts always occurred there. Most commonly, all four animals would convene in their respective “conflict corners” at the same time. There, they would sit or hang close to the wire-mesh, facing the other group and intensely staring at their counterparts (similar to the “arched brows” pattern in *Hylobates lar*, Baldwin and Teleki, 1976, p. 33). From time to time, they forcefully threw back their body without letting loose of the wire-mesh, causing considerable noise. When even more aroused, they exhibited a repeated opening and closing of the mouth, all the time staring at the rival. Staring was frequently interrupted by defecating, urinating, and by short bouts of vigorous romping display through the cage, with animals occasionally banging both feet loudly against the wire mesh of the cage walls (*Dreidimensionale Imponierveranstaltung*, Orgeldinger, 1999, p. 75f). *Bb* and *Ra* were occasionally observed biting into the wire mesh. All four animals could simultaneously participate in conflicts, but the brachiation display was more frequently exhibited by the males. Most intimidating displays during conflicts were directed at the neighbour of the same sex (i.e., it occurred after staring at, or after an arm-pulling episode with, that particular animal).

Conflicts usually had a duration of a few minutes and were often accompanied by grunting vocalizations that occasionally developed into song bouts. All song bouts were jointly produced by both groups, and most were initiated by such more or less intense conflicts (Fig. 4). Conflict behaviour was sometimes exhibited during song bouts as well, especially during the “interlude sequences” (Geissmann, 2000). The typical siamang duet song includes a particular phrase (“SFB phrase”, Geissmann, 2000) that is usually accompanied by a vigorous brachiation display similar to those occurring during conflicts, but an obvious intra-sexual orientation was observed only during the latter.



**Fig. 1.** The siamang pair *Bb* and *Ra* (behind *Bb*) directs its calling at the neighbouring pair. Photo: Thomas Geissmann. – *Das Siamangpaar Bb und Ra (teilweise verdeckt) richtet seinen Duettgesang direkt an das Nachbarpaar (nicht im Bild).*

During conflicts, arm-pulling occurred frequently, but typically continued for only a short time (less than one minute). Afterwards, both rivals usually exhibited a short vigorous brachiation display. Arm pulling was observed exclusively between members of the same sex and appeared to occur more frequently among the males. If a female reached her arm out towards the opposite cage, she was virtually ignored by the neighbouring male. On only two occasions were *Vr* and *Bb* observed reaching their arms out towards each other. Both times *Vr* immediately withdrew her arm when the

male *Bb* tried to grab her hand, but once he briefly touched her extended hand.

## Discussion

The formation of a new pair not only resulted in changes in vocal behaviour (Geissmann, 1986, 1999), but also in other social components such as inter-group agonistic behaviour, as indicated by a significant increase in arm-pulling behaviour. The female *Vr* joined her new mate *Na* frequently and actively participated in inter-group conflicts, whereas she had rarely exhibited this behaviour before *Na*'s arrival. Apparently, she began to behave like a territorial rival and/or was recognized as such as soon as she had a mate.

A similar observation was made in northern Sumatra: "A lone male siamang was tolerated by neighbouring groups until joined by a female; conflicts occurred until the female left" (MacKinnon, cited in Chivers and Raemaekers, 1980, p. 248). In another study on white-handed gibbons (*H. lar*) in peninsular Malaysia, a lone male who frequently produced solo song bouts was tolerated by a family group in the adjacent territory. Only when a lone female began to associate and to produce duet songs with him was he repeatedly attacked by the neighbouring group (MacKinnon and MacKinnon, 1977). These authors suggest that the female song contributions added a special territorial effect to the previously tolerated song of the male.

Field experiments with playbacks of tape-recorded gibbon songs have been conducted on *H. albibarbis*, *H. lar*, and *H. muelleri* but failed to produce consistent differences in the study animals' intensity of response (e.g., orientation, approach, vocalization) to solo songs or duet songs: Responses to female solo songs were at least as intense (Mitani, 1984, 1987) or even more intense (Raemaekers and Raemaekers, 1985) than responses to duet songs, although solo singing is not typical of mated females of any of these species. Only two of the three species responded less frequently to playbacks of males than to those of duet songs (Mitani, 1984, 1987).

It is likely that two gibbons pose a more significant threat than does a solitary individual. Placing an additional siamang in a neighbouring cage, as in the present study, should be expected to elicit an increase in conflict behaviour exhibited by the resident pair, because two neighbours (the new pair) represent twice as large a stimulus as a solitary neighbour. This simple linear model, however, does not suffice to explain the observed increase in arm-pulling behaviour (0.1 events/day *versus* 3.3 events/day) by a factor of roughly 30. Apparently, a siamang pair is more than just the sum of two siamangs.

Arm pulling behaviour occurred exclusively among animals of the same sex, and in the two instances when male and female neighbours reached out toward each other were aborted before any arm-

pulling occurred. These observations support the view that territorial behaviour in siamangs and possibly in other gibbons is mostly directed toward animals of the same sex, although active territorial defence is provided predominantly by males in most gibbon species (e.g., Brockelman and Srikosamatara, 1984; Leighton, 1987).

Field experiments on white-handed (*H. lar*) and Mueller's (*H. muelleri*) gibbons also appear to support this view: In both studies, it was the male that more frequently led the group's approach to the loudspeaker when male solo songs were played to the group, and the female when female solo songs were presented (Mitani, 1984; Raemaekers and Raemaekers, 1985). This finding could not be replicated, however, on a third species, the white-bearded gibbon (*H. albibarbis*). There, group approaches were mostly led by males in both situations (Mitani, 1987). The reasons for these contradicting results are unclear. The concept of intra-sexual aggression, although supported by the present study, may be too simplistic to fully explain territorial behaviour in gibbons.

The arm-pulling behaviour observed during my study on captive siamangs is not known of wild siamangs. It may be a substitute of the behaviour normally occurring during inter-group-encounters in wild siamangs, as described by Chivers (1974). The chasing and displays occurring in such situations (see introduction) may allow the neighbours to assess each other's fitness, fighting ability, pair-bond strength and/or determination to defend the territory. These interactions between territory holders appear to be ritualised and only rarely end in fights with physical contact (which would be highly dangerous because the siamangs' long, dagger-like canines make formidable weapons). In the present study, the cages not only prevent the siamangs from chasing each other across the territory boundary but, at the same time, prevent them from leaving that same area. This artificial situation may have provoked the more physical arm-pulling behaviour observed during the present study, and may also be responsible for keeping the number of the territorial interactions at a consistently high level even two months after the initial formation of the new pair.

## Acknowledgements

I thank the curators and staff members of the Seeteufel Zoo in Studen for permission to study the gibbons at their facility. I am grateful to Lori Sheeran, Elke Zimmermann, Robert Dallmann and two anonymous reviewers for reading and commenting on this manuscript.

## References

- Baldwin, L. A., and Teleki, G. (1976). Patterns of gibbon behavior on Hall's Island, Bermuda. A preliminary ethogram for *Hylobates lar*. In Rumbaugh, D. M. (ed.), *Gibbon and siamang*, vol. 4, Karger, Basel and New York, pp. 21-105.
- Brockelman, W. Y., and Srikosamatara, S. (1984). Maintenance and evolution of social structure in gibbons. In Preuschoft, H., Chivers, D. J., Brockelman, W. Y., and Creel, N. (eds.), *The lesser apes. Evolutionary and behavioural biology*, Edinburgh University Press, Edinburgh, pp. 298-323.
- Chivers, D. J. (1974). *The siamang in Malaya – A field study of a primate in tropical rain forest (Contributions to primatology vol. 4)*, Karger, Basel and New York, 335 pp.
- Chivers, D. J., and Raemaekers, J. J. (1980). Long-term changes in behaviour. In Chivers, D. J. (ed.), *Malayan forest primates: Ten years' study in tropical rain forest*, Plenum Press, New York and London, pp. 209-260.
- Geissmann, T. (1986). Mate change enhances duetting activity in the siamang gibbon (*Hylobates syndactylus*). *Behaviour* **96**: 17-27.
- Geissmann, T. (1999). Duet songs of the siamang, *Hylobates syndactylus*: II. Testing the pair-bonding hypothesis during a partner exchange. *Behaviour* **136**: 1005-1039.
- Geissmann, T. (2000). Duet songs of the siamang, *Hylobates syndactylus*: I. Structure and organisation. *Primate Report* **56**: 33-60.
- Gittins, S. P. (1984). Territorial advertisement and defence in gibbons. In Preuschoft, H., Chivers, D. J., Brockelman, W. Y., and Creel, N. (eds.), *The lesser apes. Evolutionary and behavioural biology*, Edinburgh University Press, Edinburgh, pp. 420-424.
- Gittins, S. P., and Raemaekers, J. J. (1980). Siamang, lar and agile gibbons. In Chivers, D. J. (ed.), *Malayan forest primates – Ten years' study in tropical rain forest*, Plenum Press, New York, pp. 63-105.
- Ibscher, L. (1964). *Verhaltensstudien an Weisshandgibbons (Hylobates lar) im Zürcher Zoologischen Garten*, Diploma thesis, Zoologisches Institut, Universität Zürich, 78 pp.
- Leighton, D. R. (1987). Gibbons: Territoriality and monogamy. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate societies*, University of Chicago Press, Chicago and London, pp. 135-145.
- MacKinnon, J., and MacKinnon, K. (1977). The formation of a new gibbon group. *Primates* **18**: 701-708.
- Mitani, J. C. (1984). The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). *Behavioral Ecology and Sociobiology* **15**: 225-229.
- Mitani, J. C. (1987). Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behavioral Ecology and Sociobiology* **20**: 265-269.
- Orgeldinger, M. (1996). Territorial behaviour in captive siamangs (*Hylobates syndactylus*). *Primate Report* **44**: 34-35 (Abstract only).
- Orgeldinger, M. (1999). *Paarbeziehung beim Siamang-Gibbon (Hylobates syndactylus) im Zoo. Untersuchung über den Einfluss von Jungtieren auf die Paarbindung*, Schöling Verlag, Münster, 317 pp.
- Raemaekers, J. J., and Raemaekers, P. M. (1985). Field playback of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species-specific responses. *Animal Behaviour* **33**: 481-493.
- Siegel S., (1956). *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York and London.

## Zusammenfassung

**Konflikte zwischen zwei Gruppen von Siamangs (*Symphalangus syndactylus*) im Zoo**

In der vorliegenden Studie wird das territoriale Verhalten von Siamangs vor und nach der Bildung eines neuen Paares untersucht. Ursprünglich lebte in einem Käfig ein etabliertes Paar, im benachbarten Käfig ein erwachsenes Weibchen. Nachdem im zweiten Käfig durch Zugabe eines adulten Männchens ein neues Paar gebildet wurde, stieg das territoriale Verhalten zwischen den beiden Gruppen sprunghaft an. Dies äusserte sich unter anderem in einem Anstieg der Duettsänge beider Gruppen, aber auch in aggressiven Verhaltensweisen zwischen den Gruppen, wie dem "Armziehen", einer von Gibbons bisher nicht beschriebenen Verhaltensweise. Das Armziehen wurde ausschliesslich zwischen gleichgeschlechtlichen Tieren gezeigt. Der Anstieg des territorialen Verhaltens lässt sich nicht vollständig dadurch erklären, dass ein territoriales Tier mehr vorhanden war, sondern scheint direkt mit der Bildung eines neuen Paares zusammenzuhängen.